Hibbard-Influence of tension on formation of mechanical tissue in plants

THE INFLUENCE OF TENSION ON THE FORMATION OF MECHANICAL TISSUE IN PLANTS

A THESIS

SUBMITTED TO THE FACULTY OF THE DEPARTMENT OF LITERATURE
SCIENCE AND THE ARTS OF THE UNIVERSITY OF MICHIGAN
FOR THE DEGREE OF DOCTOR OF
PHILOSOPHY

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Reprinted from the
BOTANICAL GAZETTE, Vol. XLIII, No. 6, pp. 361–382
June, 1907

Composed and Printed By
The University of Chicago Press
Chicago, Illinois, U. S. A.

VOLUME XLIII NUMBER 6

BOTANICAL GAZETTE

JUNE 1907

THE INFLUENCE OF TENSION ON THE FORMATION OF MECHANICAL TISSUE IN PLANTS[1]

RUFUS PERCIVAL HIBBARD

The radical change from a theory of self-regulatory development of mechanical tissue in plants subjected to tension by pull, to one implying no reaction whatever, necessitates detailed evidence before the latter can be accepted. The following investigation was directed to a more complete knowledge of the reactions of a plant to tension, to determine if possible what influence this exerts on the formation of mechanical tissue. Heretofore the root system has been entirely ignored, but this together with the stem has been included in the work here recorded.

I. Historical

For some time previous to 1891, physiologists had generally assumed that a plant reacted to a gradually increasing strain by a development of its mechanical tissue. HEGLER (PFEFFER '91) in this year subjected several stems and leaves to a longitudinal pull. In response to this method of experimentation, the plant, according to HEGLER, withstood greater strain than one grown under normal conditions. For example, a seedling of *Helianthus annuus* whose original breaking strength was 160^{gm} had a breaking strength of 250^{gm} after two days under the influence of a pull of 150^{gm}. The petioles of *Helleborus niger*, which at first could withstand a weight of only 400^{gm}, after five days, during which the weights had been gradually increased, held without breaking 3.5^{kg}, while those under normal conditions gained but little strength in the same time. Marked differences were

[1] Contribution 92 from the Botanical Laboratory of the University of Michigan.

apparent, not only in the tensile strength, but also in anatomical structure. On examination of various sections, HEGLER noticed (1) a numerical increase in the cells of the collenchyma; (2) an increased thickness of the walls of the collenchyma, sclerenchyma, and bast; and (3) the production of entirely new tissues. These observations led him to the conclusion that a plant responds to a gradually increasing strain by a development of mechanical tissue. It is indeed unfortunate that only a preliminary report of HEGLER's work can be had. The influence that his conclusions exerted has been widely felt, and the principles laid down were widely accepted.

RICHTER ('94) concluded that when the stems of Chara were pulled longitudinally, there was an increase of strength. Thus, in his opinion, he confirmed the observations and results of HEGLER. But we may dispose of this interpretation in the words of BALL (:04), who says: "Die Resultate RICHTERS sind etwas zweifelhaft, da er keinen Vergleich zwischen belasteten Chara-Pflanzen und unbelasteten von demselben Alter und derselber Grösse gegeben hat."

VON DERSCHAU ('94) came to the conclusion that a gradually increasing pull without contact on certain twining petioles raises the breaking strength, increases the development of mechanical tissue, and calls forth the development of new tissue. His first statement is borne out by experiments which show that even after twenty-four hours the plant part under strain could withstand a weight which at first would have broken it. From a study of sections of the various petioles, he found that marked anatomical differences occurred. There was a numerical increase in almost all kinds of cells. The bast thickened in all the petioles examined except those of *Solanum jasminoides*, and the ring of vascular bundles was made complete in all but Solanum, where it was half-moon shape, as in the normal petioles.

Concerning tendrils no experiments have been recorded to determine the effect of pull alone on the free basal portion. PENHALLOW ('86, p. 49) noted that tendrils that had secured attachment were larger, stronger, and more rigid, from which it would appear probable that contact produces a more or less marked effect in accelerating or at least in increasing the strength of parts. This view gains strong confirmation from similar conditions in Ampelopsis.

WORGITZKY ('87), in his "Vergleichende Anatomie der Ranken," gives the results of weighting experiments, and comes to the same conclusions as VON DERSCHAU. He found, by comparing weighted tendrils of *Passiflora quadrangularis* which had secured attachment with weighted tendrils which had not, that the tensile strength of the former had increased about twice as much. With tendrils of *Curcurbita Pepo* the resistance to strain was increased thirteen fold. This he believed was not the result of pull alone, but one of pull and contact combined.

NEWCOMBE ('95, p. 446), speaking of the reaction of tendrils to contact, states "that the first strengthening tissue is here laid down as a response to contact; its increase is the regulatory response of the plant to the strain that it feels."

MACDOUGAL ('96, pp. 377, 378) believes that contact stimuli are not transmitted beyond 2 or 3^{mm} and, as the thickening of the tendril always takes place after contact, we are left to conclude that it is due to the pull or traction exerted by the weight of the stem supported by the tendril.

PEIRCE (:04, p. 241) believes also that the strengthening of the free basal portion is not due to contact, but to the pull exerted in bringing the stem nearer the support.

FITTING (:03, p. 476) has lately shown that contact stimuli are transmitted for some distance, and for that and other reasons their effect on the basal portion of the tendrils cannot be excluded. It thus becomes a question how much of the increase of strength is due to pull and how much to contact.

VÖCHTING (:02) investigated the influence of pull on sunflowers and cabbages that had been prevented from flowering by means of decapitation, and found that no new tissue had been formed and that no increase of mechanical tissue had occurred as a result of the pull.

WIEDERSHEIM (:03) finds that the expected development of new tissue and the thickening of the wood and bast fibers in weighted pendent branches of Fraxinus, Fagus, Sorbus, and Ulmus does not occur. On the other hand, in Corylus he observed an increase in the number of bast fibers. This he attributes to a self-regulatory development.

BALL (:04) repeated the work of HEGLER. As a result of numerous

experiments to determine exact conditions, he has been able to show that in general the breaking strength of a plant stem does not increase in response to a gradually increasing pull, and that no increase of breaking strength follows as a result of pull on a stem growing in a horizontal plane. Detailed examinations of microtomic and free-hand sections, stained and unstained, show that there is, as a result of pull, no increase in the thickness of the walls, nor a numerical increase in the cells of the various tissues. No new tissues are produced as a result of the strain. A number of other authors, KÜSTER (p. 173), PFEFFER (:01, p. 148), and VÖCHTING (p. 282), have also failed to detect or observe any production of new tissues.

The factor of correlation has yet to be briefly mentioned. It is generally admitted by writers who have investigated the subject that a very high degree of correlation is manifest between the various organs of the plant. GOEBEL writes in his *Organography of Plants* (p. 206) "that careful research demonstrates the existence of reciprocity between parts of the plant body. . . . . The size and construction of one organ are frequently determined by those of another."

KLEIN ('86) showed that the bundles were more centrally located in the fruit stalk than in the petiole, and attributed this arrangement to the necessity for a greater mechanical strength, as well as for a more abundant supply of building material.

DENNERT ('87) on comparing the anatomical structure of the fruit stalk, before and after ripening of the fruit, found an increase in the development of mechanical tissue. This was apparent in the greater increase in the xylem and in the thickness of walls of the wood fibers.

REICHE ('87) corroborates the work of the earlier investigators and shows in many additional plants that changes in the flower stalk during its transformation to a fruit stalk go hand in hand with the development of the fruit.

PIETERS ('96) showed that although one-year-old fruit-bearing shoots of the apple and the pear had a smaller xylem cylinder in proportion to their diameters than the vegetative shoots of the same age, they were well supplied with supplementary mechanical tissues which was distributed at those points where it was most needed. In the case of the peach and the plum, the woody cylinder was larger in the fruit-bearing shoot than in the vegetative shoot. Fruit-bearing also

exerted an influence on the lignification of the cell walls of many of the tissues in the stalk. In the apple and the pear there was an abundance of well-lignified sclerenchyma and hard bast, which occurred in the vegetative shoot only sparingly, if at all.

BOODLE (:02) states that the walls of the sieve tubes and companion cells in *Helianthus annuus* become lignified as a result of strain. We also read "that the slight lignification of the parenchymatous parts of the pericycle and medullary rays unites the primary sclerenchyma strands into a more definite mechanical system attached to the strong xylem by the medullary rays." Finally, he says, "this must give greater rigidity, which no doubt is required by the heavy fruiting capitula borne by the plant."

On the other hand, in opposition to this theory, KELLER (:04) finds that pull as such does not call forth a regulatory strengthening of mechanical tissue in fruit stalks. Fruit-bearing in itself does not cause a thickening of parts nor exert an influence on the lignification of the cell walls. Upon orthotropic flower stalks, a strong or light pull in the direction of the long axis exerts no influence on the development of mechanical tissue. Displaced stalks under tension show no self-regulatory thickening, but certain anatomical changes do take place. These changes are not due to tension, but simply to the alteration in the position from orthotropic to plagiotropic, and in turn are directly referred to differences in the degree of strain between the upper and lower sides. These conclusions do not fall in line with the view that has held ground for some time, namely, that the mechanical development of the stalk goes hand in hand with the development of the fruit. Correlative growth, it is said, is no explanation for this phenomenon. This interpretation is yet to be justified. If this be true, our previous ideas must undergo transformation.

As a conclusion of the historical part of this paper I might summarize these views: Tension has no influence on the increase of mechanical tissua in any stems examined, in any petioles, nor in branches, except in *Corylus avellana*. It has some effect on twining petioles in that there occurs a thickening and lignification of certain tissues. The effect on tendrils has not yet been accurately determined. Until further data are gathered to show the contrary,

compensatory regulation or correlative growth cannot be considered as an unimportant factor.

II. Methods

The seedlings and plants examined in my work were *Helianthus annuus*, *Phaseolus multiflorus*, *Ricinus communis*, *Brassica oleracea*, *Coleus tricolor*, *Fuchsia speciosa*, and *Vinca major*. The stems compared were selected with reference to similarity in size and vigor. All tension and normal plants were grown under similar conditions.

When collected, the stems were numbered, cut into suitable lengths, and put into 50 per cent. alcohol for further examination. To study the stems, freehand cross-sections were made and the tissues measured by several methods. Further description of the different methods will be given under the proper headings.

III. Results of experimentation

A. INFLUENCE OF TENSION ON STEMS

A number of seedlings were subjected to tension in the following manner: Strong, light twine was fastened about the stem, which had previously been wound with cotton flannel to eliminate any injury due to the cord. The twine was then run over a lightly rolling pulley, hanging from a support directly above, and the weights attached to the free end of the cord. The twine was so fastened that very little injury, if any, was caused. Two loops were made from short pieces of twine, each about 30^{cm} in length. These were noosed about the stem, from opposite sides one within the other, so that four circles of twine surrounded the stem over the cloth. The ends of the loops were then connected by a short piece of twine. To this was fastened, in an adjustable manner, the cord running over the pulley. In this way, if one loop should happen to be longer than the other, an adjustment took place, so that the strain on each loop was the same, in consequence of which the stem felt the pull in the direction of its longitudinal axis.

When the seedlings were young, the unfolding leaves and growing tips might be somewhat hindered in their growth by the interference of the loops of twine. To prevent this, a strip of light whitewood, about 10^{cm} long, 3^{mm} wide, and not more than 1.5^{mm} thick, was so placed between the loops as to form a diamond-shaped figure, such as

has been described by BALL (p. 309). When the plants had reached a more advanced stage of development, this device was unnecessary, and was therefore discarded. To guard further against any possible injury that the cord might produce in the stem when heavy weights were used, the cord was frequently changed to a place above or below the original attachment.

The seeds were germinated in 20^{cm} pots containing garden loam and clay. The loam and clay were thoroughly mixed in the proportion of one of garden loam to three of clay. This gave the earth a firm cohesion, and for this reason few seedlings were uprooted. When necessary, a plaster of Paris cap was cast over the earth to the edge of the pot and securely fastened with cord. The plaster was kept from the stems by means of surrounding paper cylinders. When the seedlings had reached a height of 8 to 10^{cm}, the experiments were usually begun, although in some cases they were allowed to grow stronger and taller before being subjected to tension.

There are two ways to determine whether or not tension has increased mechanical tissue. First, by a measurement of the breaking strength, and second, by the observation of the size of the various tissues and the thickness of the cell walls. The first method has been followed admirably on various stems by BALL. Beyond a few experiments performed by the writer, the need of further observations by this method seems quite unnecessary.

To determine by microscopic means the differences between tension and normal plants in the mechanical tissues, several methods were used. One method was to determine the thickness of tissues and walls by an ocular micrometer. The areas of the woody cylinders were computed by making camera-lucida drawings of the xylem, and the areas of these irregular drawings were determined by means of a polar planimeter. A third method was devised of making camera drawings of the woody cylinder on Bristol board, which were then carefully cut out and weighed on a chemical balance. A fourth method consisted in comparing the phloem bundles of the tension and normal plants. The number of bast fibers in cross-section of a tension plant was compared with that in the bundles of the normal plant. The number of bundles in one was directly compared with the number in the other. A fifth method consisted in comparing

sections of the tension-plant stem above and below the place of attachment of the cord, to note any differences in anatomical structure in the two regions.

Helianthus annuus (greenhouse cultures)

Ten plants of *Helianthus annuus* that had grown in the greenhouse for a month were weighted on November 4 with 50^{gm}. On the third day following, the weight was increased to 100^{gm}, and on the tenth to 200^{gm}. At this time the attachments were changed to a place above the original one. This, as has been mentioned above, was for the purpose of guarding against injury due to the cord. Additional weights were added at various times, until in this set of experiments the final amount reached 600^{gm} on November 23.

At this time the weights were removed from five plants and the stems placed in 50 per cent. alcohol. Five plants that had grown under similar conditions, except that they had not been subjected to tension, were also gathered to serve as controls. These controls had been chosen at the beginning of the experiment and were closely watched throughout the time of experimentation in order that all conditions other than tension should be the same.

Cross-sections of the normal stem of *Helianthus annuus* of this age, at a height of 7^{cm} from the ground, do not show a completely closed xylem ring. The bundles are separate and are of various sizes. The secondary xylem is beginning to form.

Sections for microscopical study were made at a place 7^{cm} above the first lateral root in both tension and normal plants. The place of attachment of the cord on the tension plant was some distance above this, so the sections were within the region of tension. Careful observations by two persons, working independently, did not disclose any appreciable difference between tension and normal plants.

Other sections were then made in the tension stem above and below the attachment. No appreciable differences are detected when sections in the tension region are compared with sections on the same plant out of the region of tension.

As a general result of observations of the first five plants, we may say that tension exerted upon the stem along its longitudinal axis did not call forth a self-regulatory development of mechanical tissue.

The remaining five plants of the ten used in the above experiment were allowed to grow with the constant pull of weights until they had produced flowers. The purpose of this experiment was to note the influence of tension continued for a long period. These plants because of the winter season were rather weak. Cross-sections of these stems at 7^{cm} above the ground show a closed xylem ring. The area and weight methods as described above were employed for detecting differences. Even in these examples we find no self-regulatory development of mechanical tissue in response to tension, nor are the results on old stems any different from those on young ones. The final weight carried by each plant was 2300^{gm}.

The above experiments on *Helianthus annuus* were repeated with twenty-five other individuals and the same methods for detecting differences were used. Only a few of these plants were allowed to mature, as young plants give just as reliable results and are much more easily handled. The duration of the experiments varied from two to four weeks. The final weights varied from 600^{gm} to 2860 . The general result was that tension, gradually increased and in the direction of the longitudinal axis, did not induce a self-regulatory development of mechanical tissue in the sunflower stem. In this we agree fully with the results of BALL.

Helianthus annuus (field cultures)

Seventeen sunflower plants were subjected to the same condition of strain, but to other external conditions which were not so uniform as those in the greenhouse. These experiments were conducted in the open field during the months of July and August 1905.

An examination of the cross-sections of these stems, taken at 1^{cm} above the first lateral root, gives the general result that was found to be true in the case of the plants grown in the greenhouse, namely, that an increasing tension along the longitudinal axis does not call forth a self-regulatory development of mechanical tissue in the sunflower stem. By the area method only three tension plants show an increase of mechanical tissue over that of the controls. Two control plants show an increase in mechanical tissue over that of the tension. The others show slight differences that fall within the limit of error. Ten examples from the seventeen are given in Table I.

TABLE I

Plant	Tension	Normal	Percentages (Normal = 100)
No. 1 A.	29.87 sq. cm.	31.16 sq. cm.	− 4
No. 2 B.	42.45	42.71	− 6
No. 3 B.	17.42	17.29	8
No. 4 B.	23.74	23.23	2
No. 5 B.	35.62	54.52	−53
No. 10 B.	33.68	51.81	−54
No. 9 A.	53.16	31.81	67
No. 5 A.	56.13	36.45	54
No. 8 A.	55.04	49.42	11
No. 1 B.	34.65	32.65	6

In the above table the second column contains the measurements of the relative area of xylem in the tension plant in section; the third column contains similar measurements in the control plants in section; and the fourth column contains percentage differences when the normal is taken as 100.

Ricinus communis (field cultures)

The same experiments were made upon Ricinus stems, which were also cultivated in the open field during the summer months. Seventeen, chosen at random, from the large number that were put under tension, showed after close observations the same general results as previously indicated for Helianthus. There is no constant increase in mechanical tissues as a result of a gradually increasing pull. The following table shows results of observations on ten plants.

TABLE II

Plant	Tension	Normal	Percentages (Normal = 1)
No. 1 A.	24.20 sq. cm.	17.10 sq. cm.	42
No. 2 A.	59.615	39.87	50
No. 3 A.	26.45	23.915	11
No. 5 A.	52.50	59.9	−14
No. 9 A.	52.39	56.555	− 8
No. 10 A.	45.00	55.7	−24
No. 3 B.	30.10	24.6	23
No. 4 B.	35.30	33.9	4
No. 5 B.	15.80	15.40	3
No. 7 B.	50.30	48.70	3

Nos. 1A, 2A, 3A, and 3B show results in favor of tension plants; nos. 5A and 10A show results in favor of normal plants; nos. 9A,

4B, 5B, and 7B are within the limit of error. The remaining seven of the original seventeen were estimated with the aid of the microscope. These in nowise alter the general conclusion.

Vinca major (greenhouse cultures)

Twenty-three thrifty young stems of *Vinca major*, some of which were still growing upright, and others that had already bent over and were growing in the usual drooping way, were subjected to tension by means of weights. The young upright stems were placed under tension in the same manner as explained above for *Helianthus annuus*. The pendent stems were placed under tension by hanging the weights upon them without the use of the pulley. Cotton flannel was wound around the stem just above a node. Two loops of twine were then noosed around the stem over the cloth, and drawn tight. From the end of each noose hung equal weights, and thus the stem received the strain along its longitudinal axis.

The duration of the experiments on the upright stems varied from two to four weeks, and the final weights varied from 1250 to 1500^{gm}. The duration of the experiments on the pendent stems varied from eleven to twenty-eight days, and the final weights varied from 1000 to 1500^{gm}. Normally growing stems for comparison with tension stems were selected with regard to similarity in diameter, length, manner of growth, and vigor. In most cases sections were taken in normal and experimental plants at equal distances from the stem apex.

Observations with a magnification of 100 diameters show that in the majority of plants the whole xylem ring is thicker and composed of thicker-walled cells in the tension plant. The bast is more abundant in the tension plant. Under a higher magnification of 150 diameters, it is noticed that the walls of the bast fibers are thicker in the tension plant.

In all of the twenty-three plant stems under tension, five only do not show an increase in the absolute size of the xylem or in the thickness of the cell walls of bast or xylem. The following tables give the results obtained for a few of the representative plants and their controls. The preponderance of evidence, judging from the number of plants experimented on, shows that an increase in the quantity of xylem amounts to at least 50 per cent. In the table, T indicates

tension plant, and N the control. The areas given are those measured on the drawings.

TABLE III (AREA METHOD)

Plant	Area of whole section	Area of xylem and pith	Area of xylem	Percentages
No. 2A. T.	97.75 sq. cm.	35.62 sq. cm.	15.29 sq. cm.	53
No. 2A. N.	97.62	34.32	10.00	
No. 3 T.	153.49	60.64	20.13	82
No. 3 N.	154.20	61.62	11.03	
No. 2B. T.	129.49	53.75	14.65	− 3
No. 2B. N.	125.10	50.13	15.03	

The last plant (no. 2B. T) is one of three mentioned above. This shows a slight difference in favor of the normal and by so much weakens the general conclusion.

The first four plants of the preceding table were used to test the differences by the weighting method. The two methods show results which are very close, only varying by 2 per cent. to 4 per cent.

TABLE IV (WEIGHT METHOD)

Plant	Weight of drawing of cross-section	Weight of xylem	Percentages Difference
No. 2 T.	1.87 gm	0.28 gm	49
No. 2 N.	1.89	0.19	
No. 3 T.	2.8641	0.382	78
No. 3 N.	2.9301	0.215	

Brassica oleracea (greenhouse cultures)

Five plants of *Brassica oleracea* were put under tension in a similar way as explained for *Helianthus annuus*. The seeds were planted in 20^{cm} pots and placed in the greenhouse. In a little more than a month these had grown sufficiently for experimentation, being about 7^{cm} tall. The original weight for each plant was 50^{gm}; this was gradually increased until the final weight reached 1000^{gm}. The duration of the experiment was two weeks.

Sections were made freehand at places 5^{cm} and 1^{cm} above the ground in both control and tension plants. An examination of the various anatomical structures failed to show any constant differences between the control and experimental plants. The xylem ring in the

tension plant when compared with the xylem ring in the control plant showed no appreciable difference. The phloem in each had developed to the same degree. Under high power the walls of the cells in the tension plant were seen to be no thicker than the walls of the corresponding cells of the normal plant.

A further study, such as has been made with other stems by determining differences with the aid of area or weight methods, seemed unnecessary. It must be concluded then, as a result of experiments on five plants of *Brassica oleracea*, that tension does not call forth a self-regulatory development of mechanical tissue.

Phaseolus multiflorus (greenhouse cultures)

Four plants of *Phaseolus multiflorus* were subjected to tension for two weeks. These plants were cultivated in the greenhouse and when a few centimeters high were put under a strain in the same manner as explained for Helianthus. Small weights were first attached, and to these were added others until the final weight amounted to 1750^{gm}. Freehand sections were made at heights on the stem 5^{cm} above the ground. Sections at corresponding places in the control plants were chosen for comparison. Control plants, as in all experiments, were selected with reference to similarity in growth, size, and vigor.

In cross-section the stem of Phaseolus shows a very well-differentiated xylem ring, and it is very easy to note differences if they occur, when tension and control plants are compared. In the four plants under experimentation, a careful inspection with the microscope failed to show any appreciable differences in the size of the xylem ring, bundles of phloem, or thickness of walls. For this reason it seemed unnecessary to proceed with the various methods as used in previous experiments. My conclusion, therefore, with reference to the influence of tension on the stem of *Phaseolus multiflorus* can be nothing else than that tension does not induce a self-regulatory development of mechanical tissue.

Conclusion

From the above seven experiments we conclude that tension has no influence in the formation of tissue in stems of *Helianthus annuus*, *Ricinus communis*, *Brassica oleracea*, and *Phaseolus multiflorus*, but that in Vinca it seems to call forth a regulatory development of sup-

porting tissues. This shows itself in an increase in the amount of xylem and in the thickness of the cell walls of the same.

INFLUENCE OF COMPRESSION ON STEMS

In my experiments I made use of the following plants and seedlings, which were cultivated in the greenhouse: *Helianthus annuus*, *Vinca major*, *Fuchsia speciosa*, and *Coleus tricolor*. The controls were raised in the same place, and received the same care and attention as the plants under experimentation.

A number of the above-named plants and seedlings, young and old, were subjected to compression by various means. The most common means was that of fastening the weights directly upon the stem. Around the stem, some distance above the ground, usually not more than 15^{cm}, a strip of cotton flannel was wound. Over this and around the stem from opposite sides were noosed two loops in the manner already described in the tension experiments on Helianthus, Vinca, etc. Equal weights were attached to each loop, so that the strain was uniform on the opposite sides of the stem. To insure the stem from bending under the weight, bamboo stakes were driven into the ground close to the plant and then fastened to it in two places, one above and one below the place from which the weight hung, but so fastened as not to free the plant from the compression of the weights.

In other cases the compression was narrowly localized. This regional compression was brought about in the following manner: Weights were hung from the sides of the stem as has already been explained. Below the attachment of these weights, some 10^{cm} distant, a strong cord was fastened about the stem in the manner as described for the tension experiments. This cord was run over a pulley fixed to a support directly above, and to the distal end of the cord were fastened weights equal to those hanging on the plant. By this method, a weight above pressing down and another below pulling up, there was a compressed region; while the upper and lower parts of the stem were free from compression.

Variation in the method of hanging the weights on the plants was employed, but these details are of minor importance, and will not be given here.

Helianthus annuus

Twenty-six sunflowers were subjected to compression by the different methods explained above, the method depending upon the size and age of the plant used. Seedlings were cultivated in 20^{cm} pots in the greenhouse. The duration of the experiments varied from two to five weeks. The weights varied from 400 to 2100^{gm}. As a general result of this experiment one may say that a compression strain will call forth slightly increased mechanical development in a majority of the plants used. This expresses itself in a slightly greater thickness of cell wall and xylem cylinder. The phloem bundles are also slightly larger.

Fuchsia speciosa

Five small Fuchsia stems were subjected to a compression strain of 185^{gm}. No bending was present to modify the anatomical structures. Sections were taken from the stems within the region of compression at distances from the ground varying from 5 to 8.5^{cm}. Sections of the normal stems taken at corresponding places were selected for comparison. With the aid of an eye-piece micrometer, measurements of the xylem cylinders were made in two directions at right angles to each other. The average of these two measurements was taken as the average width of the xylem ring. Data so obtained indicated a greater thickness of xylem in the tension plant than in the control, but the increased mechanical development was not strong.

Vinca major

Eight young upright Vinca stems were subjected to compression by hanging the weights upon them. To prevent bending, the plants were tied to a support in the usual way, the final weight carried by each plant being 200^{gm}. The period of experimentation extended from March 10 to March 25. Control plants were selected with reference to the same age, growth, and vigor. Sections taken in the region of stress were compared with sections taken at corresponding places in normal plants.

Observations under the microscope indicated, in a majority of the plants experimented upon, that a compression strain causes slightly increased development of mechanical tissue.

Coleus tricolor

Four young and thrifty Coleus plants were put under compression in a similar manner as explained for Fuchsia. After a period of twelve days under a compression strain of 225^{gm}, they were gathered and together with their controls were placed in 50 per cent. alcohol for examination later.

Observations under a magnification of 150 diameters revealed no evidence of any differences between control and tension plants. We are hardly justified, then, in concluding that in these Coleus plants compression exerts any influence toward a development of mechanical tissue. For reasons that are apparent, the absolute amounts of xylem in both normal and tension plants were not determined by either the area or weight methods. The conclusion drawn was the result of detailed observations under the microscope by two persons working independently.

Conclusion

The foregoing experiments were performed to determine the influence of longitudinal compression upon the formation of mechanical tissue in the stems of *Helianthus annuus*, Vinca, Fuchsia, and Coleus. The results indicate that the stems of all the above-named plants except Coleus reacted to a compression strain by a self-regulatory development of mechanical tissue, yet the evidence cannot be called conclusive.

C. INFLUENCE OF TENSION ON THE ROOT SYSTEM

A number of papers on the influence of pull, or tension, on stems, petioles, and other aerial organs have been published, but nothing as yet has reached print concerning the influence of this treatment on the root system. It is the purpose of this section of the paper to give the results of experiments along this line, and to show that in the root system we have an organ that reacts to tension by a self-regulatory development of mechanical tissue.

Tension on the root system was applied by means of a pull upon the stem, brought about in the usual way by weights, when the seedlings had grown to a height of about 15^{cm} and the first pair of leaves had fully developed.

The seeds for any one series of experiments on *Helianthus annuus*

were chosen from the same head. No further selection was made. The Ricinus seeds were all taken from one variety. All the seedlings used for these experiments, except where otherwise indicated, were cultivated in an open field during the summer of 1905. The ground was carefully prepared with a mixture of clay, swamp muck, and manure. This was thoroughly spaded, and afforded a rich, firm soil, from which the seedlings were not easily uprooted when under tension.

Two series of experiments were run through, one in the earlier and the other in the later part of the summer. The duration of the experiments was generally two weeks, after which time the plants were dug up, together with their controls, and their root systems carefully washed and placed in 50 per cent. alcohol. The root systems of control and tension plants were first compared with reference to their external form and size and later with reference to their internal structures. The control plants were chosen from the same locality in which the plants under experimentation were grown and were selected with reference to similarity in size and vigor.

I. EXTERNAL ROOT FORM

To determine the influence of tension on the root system, a careful and close comparison was made between the control and tension plants. Special attention was given to observations upon the main and secondary roots. At times it was noticed that the lateral roots attained a greater development on account of the small or aborted growth of the main root. On the other hand, the main root would sometimes reach quite an enormous growth, in consequence of which the lateral roots would not attain the usual size. This great growth of the main root occurred far less frequently than that of the lateral roots. Thus what may be called a compensatory regulation holds true with reference to these two orders of roots. This compensatory regulation, then, must not be confused with the evident strengthening and increased development of roots due to tension. In our comparisons of the normal and tension plants this fact had always to be kept in mind.

The number, average length, and generally vigorous condition of the roots and rootlets were determined. It was found that in general the main root of the tension plant was straighter, tapered more

gradually, and attained greater length; the lateral roots were generally more numerous, larger in cross-section, straighter, and longer. The greatest growth of lateral roots was always found at the crown of the main root near the surface of the ground.

Helianthus annuus

To show the differences in root form between the normal and tension plants, two series of experiments were made on *Helianthus annuus*. The results of both were in general the same. All plants compared were of the same size and were grown in the open field under similar conditions. The first series was under experiment from July 8 to July 21, the second from September 21 to October 10. The final weights to which the plants were subjected varied from 750 to 1000^{gm}.

The following are observations obtained from a comparison of the root systems of two seedlings of the same relative size and vigor. These were representative seedlings and the results obtained were characteristic of the entire set of thirty-four plants: The main root of the tension plant was straight for a distance of 6^{cm}, that of the control plant undulate throughout its whole course. The main roots had the same diameter at the upper ends. At 5^{cm} below the first lateral root, the diameter of the tension plant was 3^{mm}; while that of the normal plant was 2^{mm}. The normal plant had a cluster of 10 lateral roots at the upper end with a diameter of 1^{mm} or more; while the tension plant had at its upper end a cluster of 13 lateral roots with a diameter of 1^{mm} or more. All these were longer, much more branched, and in general appearance stronger than the lateral roots in the normal plant.

Here the differences between normal and tension plants were very marked, and it will be noticed later that marked differences appear as a result of microscopic observations.

Ricinus communis

The same general differences in external root form are noticeable in *Ricinus communis*. With this, as with the sunflower, two series of experiments were run through. The first was under experimentation from July 5 to July 21, and the second from September 26 to

August 11. The final weights held by the plants under tension varied from 1800 to 2000^{gm}.

The results of a comparison of two plants of *Ricinus communis*, selected with reference to similarity in all respects except in the matter of tension, are added below. The results here obtained are in general the same in the other sixty-seven plants used in the experiment.

The main root of the tension plant was straight throughout its whole course, that of the control undulate. The main roots had the same diameter at the upper ends. At 5^{mm} below the first lateral root the diameter of the tension plant was 4^{mm}, while that of the control was 3^{mm}. The control plant had a cluster of 18 lateral roots at the upper end with a diameter of 1^{mm} or *less;* while the tension plant had at its upper end a cluster of 23 lateral roots with a diameter of 1^{mm} or *more.* The lateral roots in the tension plant were much longer than those of the control plant. The root system of the tension plant was noticeably stronger in general appearance.

The results of these experiments on seedlings of *Ricinus communis* show how different the root systems of the plants under tension are from those growing under normal conditions. In every respect the differences are quite marked. Similar experiments conducted in the greenhouse with both Helianthus and Ricinus plants show like results.

From the above data one may conclude that tension causes a thickening and strengthening of the roots of *Helianthus annuus* and *Ricinus communis* grown in the open or in the greenhouse.

2. INTERNAL ROOT STRUCTURE

For a study of the internal root structure, freehand sections of the main and lateral roots were made. Sections of the main root were generally taken in two places, one near the top and the other some distance below. Sections of the lateral roots were made 1 to 2^{mm} from their insertion on the main root. The lateral roots to be sectioned were taken from the upper cluster of rootlets or from a position on the main root not lower than 1^{cm} from the first large lateral root. More than one lateral root on each plant was sectioned so as to obtain average results. The strongest and the average rootlets were always selected for comparison. No rootlet was chosen

unless it looked healthy, reached a fair length, and had a number of branches. Often the largest lateral root of the normal plant was not so large as the largest in the tension plant. This was sometimes taken as evidence of greater growth due to tension, but the results were not based on this fact alone. From the tension plant was selected a rootlet which was as large and vigorous as the largest rootlet in the normal plant. A comparison could then be made and the results, whatever they were, could be accepted without further allowance or additional estimation.

Helianthus annuus

Sections were taken of the main root at various points below the first lateral root. These were compared with sections taken at corresponding places in the control plant. The diameters of the sections of the normal root averaged 1^{mm} greater, and for this reason a better mechanical growth would be expected in the control. As the result of careful observations the xylem was found to be greater in amount and the cells were thicker-walled in the tension plant than in the normal. In cases where the diameter of the sections of the normal and tension roots were the same, the tension root always showed the greater amount of xylem and thicker-walled cells.

From a comparison of the rootlets at the crown of the main roots of the tension plants with those from the corresponding place in the control plants, it was seen that the former had a larger size, and microscopical study emphasized this fact and showed that the xylem cylinder was larger and the walls of the cells thicker in the tension plants. Rootlets of average size taken from tension plants were compared with others of the same size, vigor, and growth taken from the normal plants. The comparison showed that the tension plants had a larger amount of xylem and cells with thicker walls.

To recapitulate, we may say that, out of five Helianthus plants under tension, the main roots of all show a better development of mechanical tissue than the main roots of five control plants of similar development. With reference to the lateral roots, the majority in the experimental plants showed a better mechanical development than similar rootlets in the control plants.

Ricinus communis

It may be said by way of summary that twenty-five out of the thirty-four Ricinus plants under tension in this series show a greater development of mechanical tissue in both the main and lateral roots than in the control plants. Sections of the primary roots show considerable differences, while the secondary roots show some but not so great differences in favor of the tension plants.

Helianthus annuus

The plants for comparison were chosen from the series of experiments in the open field during the latter part of the summer. The evidence obtained from observations upon the main roots of twelve seedlings of *Helianthus annuus* shows that nine reacted to tension by an increased development of mechanical tissue, while all the lateral roots examined showed a greater development of mechanical tissue in the tension plants.

IV. Summary

In the foregoing work, of the five stems tested for the increase of mechanical tissue under the influence of longitudinal pull, only that of Vinca showed a response, and in this the increase was not great.

Pull in the direction of the longitudinal axis of the plant called forth a small increase of mechanical tissue in the main and lateral roots of *Helianthus annuus* and *Ricinus communis*.

Compression tension brought small increases of mechanical tissue in the stems of Fuchsia, Vinca, and Helianthus. By the same method Coleus gave no response.

The investigation, the results of which are here recorded, was carried out under the direction of Professor F. C. NEWCOMBE, to whom I wish to express my grateful thanks for kindly encouragement and helpful suggestions.

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